主論文

Doctoral thesis

Title:

Community ecology of floral resource partitioning by eusocial bees in an Asian tropical rainforest

Author:

Teruyoshi NAGAMITSU

Center for Ecological Research, Kyoto University

Shimosakamoto, Otsu, Shiga 520-01, Japan

March 1998

Summary

Tropical eusocial bees, stingless bees and honey bees, which are main pollinators of rainforest plants, have been regarded as generalists with high interspecific overlap in floral resource use. This study shows that eusocial bee species partitioned floral resources in a rainforest in Sarawak, Malaysia, and that variations in foraging tratis and heterogenieties of floral resources promoted the partitioning.

In the study site, general flowering occurred in 1992 and 1996, and population of eusocial bees changed. Honey bees disappeared during an interval between the general flowering, whereas stingless bee population was stable, but their colony foundation occurred in general flowering.

Floral resource use by stingless bees was revealed by both collection of flower visitors using a canopy observation system and identification of pollen brought to nests. The result indicated that four stingless bee species used flowers with unique features. They were 1) *Trigona melina* and *T. melanocephala* which used non-bee-pollinated plants with understory flowers, 2) *T. erythrogastra* which used solitary-bee-pollinated plants with deep flowers, and 3) aggressive *T. apicalis* which occupyed and excluded other foragers from cup- or brush-shaped flowers pollinated by eusocial bees.

Artificial feeder experiments showed that understory-flower users mainly visited lower feeders, and that aggressive species lately arrived at feeders. The latter suggests a trade-off between search and defence in eusocial bees. Replacement of early-arrived non-aggressive species with late-arrived aggressive species caused temporal partitioning at canopy flowers and artifical feeders.

Morphological analysis of mouthparts of stingless bees showed that deep-flower users had longer tongues compared to their body size. However, I did not find clear relation between sugar concentartion of nectar loads and mophology of glossae (apical parts of tongues).

In conclusion, I deduced mechanisms for spatial, temporal and morphological partitioning among eusocial bee species from variations and a trade-off in foraging traits and heterogenieties of floral resources. Further, feeder experiments, changes in foraging in general flowering activity and colony dynamics suggest interference and exploitative competition which promoted the partitioning.

200 times of those by other nectarivores, bats and hummingbirds. On the other hand, total energetic supply of nectar and pollen in rainforests has not been measured. Investment in nectar of milkweed and alfalfa was 3-5% of total photosynthetic carbohydrate product (Southwick 1984).

Though total balance between supply and consumption of floral resources is unknown in tropical rainforests, the intensive consumption by eusocial bees suggests food competition between bee populations in local scales in space and time. Invasion of Africanized honey bees, *Apis mellifera*, to the neotropics from Africa since 1956 provided a case study on effects of food competition on native bees. Africanized honey bees displaced native bees from artificial food sources and continued to forage despite harassment attacks by stingless bees (Roubik 1980). A field experiment in Panama showed that rare periods of intensive foraging by stingless bees were diminished when Africanized honey bees, which shared most pollen sources with the stingless bees, were introduced (Roubik et al. 1986). This study indicated that food harvest of stingless bee colonies would reduce to 75% of normal harvest as colony density of Africanized honey bees increased to one per square kilometer. However, experimental introduction and removal of honey bee colonies in a lowland forest in French Guiana did not change brood production and food storage of native stingless bees (Roubik 1983). Further, when Africanized honey bees invaded a native bee community in Panama, abundance of light-trapped bees did not show any noticeable changes (Wolda and Roubik 1986).

These studies confirmed that food competition reduced foraging efficiency of neotropical eusocial bees, but failed to show that competition reduced population density and individual fitness. There are clear evidences that resource harvest, particularly pollen, was positively correlated with colony brood production of eusocial bees (McLellan 1978; Roubik 1982). Thus failure to show effects of food competition on population and fitness is due to improper exmeriment design or effects of other factors, such as stochastic fluctuation, predation and competition for other resources, for example, nest sites

(Nieh and Roubik 1995) have been confirmed or suggested. If these traits have trade-offs and their variations which match resource heterogenieties, eusocial bees will partition floral resources.

1.4 Asian tropical rainforests

Food competiton and floral partitioning by eusocial bees has been studied in the Neotropics. However, Asian tropical eusocial bees have rarely been investigated except for a few studies (Koeniger and Vorwohl 1979; Inoue et al. 1985; Appanah et al. 1986; Inoue et al. 1990). In Asian tropical rainforests, food competiton and floral partitioning are expected because of some reasons shown below.

Food competition may be intense beacuse of existence of native honey bees as floral resource consumers and irregular flower shotage by unique flowering phenology, general flowering of mixed dipterocarp forests. Five native honey bee species, large *Apis dorsata*, medium *A. cerana* and *A. koshevnikovi*, and small *A. florea* and *A. andreniformis* coexist in Asian tropical rainforests, while no native honey bees exist in the Neotropics (Rutter 1988). A striking phenological feature of aseasonal rainforests in Southeast Asia is general flowering, when nearly all dipterocarps and up to 88% of canopy trees of various taxa bloom for a few months at irregular intervals of 2-10 years (Appanah 1985; Ashton et al. 1988; Appanah 1993). During the intervals between general flowering periods, these trees show little or no reproductive activity. Coexistence with honey bees and resource fluctuation with floral shotage may result in floral resource partitioning among eusocial bees in aseasonal Asian tropics.

In Asian tropical rainforests, plant species diversity and complex forest structure provide high heterogenieties of floral resources. Lowland rainforests in Sarawak, Malaysia have the highest tree species diversity and tallest canopy in the world tropics (Ashton and Hall 1992; LaFrankie et al. 1995). Floral resources in rainforests in Peninsular Malaysia are so heterogeneous that unique pollination syndromes were

2. Eusocial bees in Lambir Hills National Park

2.1 Location and climate

Study site was located in Lambir Hills National Park (LHNP), Sarawak, Malaysia (4°20'N, 113°50'E). The Canopy Biology Program in Sarawak (CBPS) marked out a canopy biology plot (200 x 400 m, 8 ha) on a clayey soil site near the headquarters of LHNP (Fig. 1). The plot is covered with intact mixed dipterocarp forests at altitude of 100 to 200 m above the sea level. The height of emergent trees exceeds 70 m. In the central part of the plot, CBPS constructed a canopy observation system with two tree towers (55 and 49 m) on neighboring ridges and nine spans of areal walkways (298 m long) connected them (Inoue et al. 1995). Using this system, CBPS study plant phenology, seasonal changes in insect abundance, and interactions between plants and animals in canopy layers since 1991 (Inoue and Hamid 1994; Inoue and Hamid 1997).

general flowering occurred.

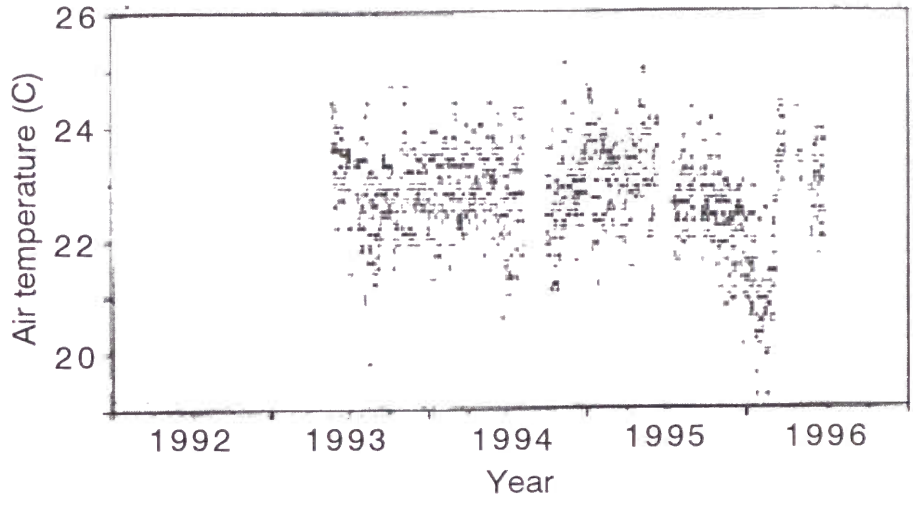

Fig. 2: Plot of daily minimum air temperature at tower 1 (Sakai et. al. 1997).

2.2 Flowering phenology and pollination syndromes

CBPS bimonthly observed flowering phenology from 1992 to 1996 along the canopy observation system and from the forest floor in the canopy biology plot (Sakai et al. 1997). In 1992, general flowering occurred, and many fruits were observed until September 1992 (Fig. 3). From October 1992 to Feburary 1996, proportion of flowering plant individuals was usually < 3.0% with a minor peak up to 6.7% in 1993. After March 1996, flowering plants rapidly increased, and proportion of flowering individuals reached 16.9% in May 1996. A lower peak was observed in October, five months after the first peak in 1996. Thus a cycle of general flowering was observed from 1992 to 1996.

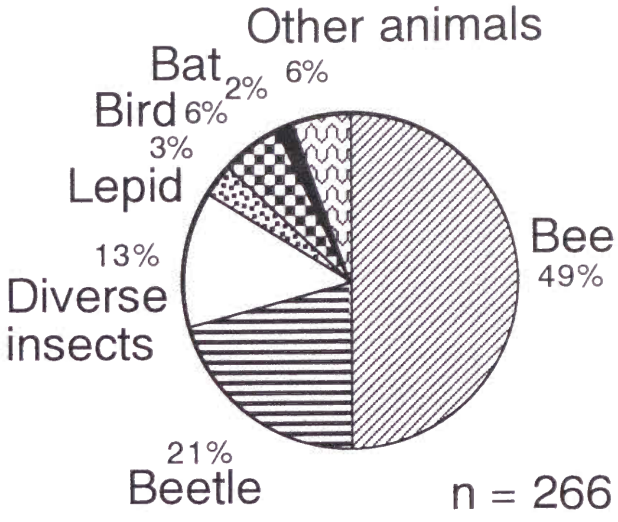

Fig. 4: Percentages of plant species pollinated by seven types of animals in Lambir Hills National Park.

2.3 Eusocial bees and colony dynamics

In Southeast Asia, the three tribes of apid bees (Apidae, Hymenoptera) are known. They are honey bees (Apini), stingelss bees (Meliponini) and bumble bees (Bombini) (Sakagami 1982). In LHNP, three species of honey bees (*Apis* spp.), 27 species and forms of stingelss bees (*Hypotrigona* and *Trigona* spp.) and no bumble see species were collected (Table 1; Inoue et al. 1994). Stingless bees are most diverse eusocial bee taxa in the tropics, and 43 species, subspecies and forms are recorded in Southeast Asia (Sakagami et al. 1990). Comparison of distribution of stingless bees shows that Borneo has the highest species diversity (33 species and forms; Inoue et al. 1994).

bees are specialized for species. Most stingless bee species nest ususally in cavities in tree trunks or branches, but occasionally in human-made cavities. *Trigona collina*, *T. rufibasalis*, *T. melina* and *T. melanocephala* nest in spaces between tree roots and the ground. Average nest volumes of stingless bee species nesting in tree cavities differ according to colony size; the two extremes were 0.3 l for *T. fuscobalteata* and 330 l for *T. canifrons* in Sumatra, Indonesia (Salmah et al. 1990).

Colony density was changes from 1992 to 1996 in LHNP according to flowering phenology. CBPS surveyed bee nests at bases of trunks of all trees with ≥40 cm diameter at 1.3 m height in the canopy biology plot, on trunks visible from towers and walkways, and in 59 wooden boxes set on the towers in 1993. Patterns of colony dynamics were different between honey bees and stingless bees (Fig. 5). After general flowering in 1992, five colonies of *Apis dorsata* disappeared from the plot, and seven colonies imigrated again in 1996. A natural nest of *A. koshevnikovi* crushed in 1993, and four colonies nested in wooden boxes in November 1996. Nests of *A. andreniformis* were not found. Hence honey bees dissappeared during rarely-flowering periods between general flowering. On the other hand, 12-15 colonies of eight stingless bee species in natural nests existed throughout a general flowering cycle. In the wooden boxes, colony foundation of *Trigona fuscobalteata* and *T. laeviceps* increased in general flowering in 1996, though the boxes were set in 1993. This pattern of colony dynamics of stinless bees suggests that natural colony density were stable in supra-annual fluctuation of floral resources, but that colony foundation was concentrated to general flowering periods.

3. Feeding guild structure

3.1 Introduction

In this chapter, I described floral resrouce use by stingless bees and showed three types of floral partitioning among these species.

To investigate floral resource use at the level of plant taxa by sympatric stingless bees, I observed their pollen diet and flower visitation, which define different aspects of floral resource use (Ranta and Lundberg 1981). Flower visitation, measured by number of collected flower-visiting bees, indicates relative intensity of floral resrouce use on each investigated plant. Thus, to estimate frequency of flower visits by each bee species requires sufficient ramdom samples of flowering plants in foraging area of the bee species. However, the random sampling is difficult due to various accessabilities to flowers of forest plants. Further, flower visits do not directly indicate floral resource use. On the other hand, pollen diet, measured by number or volume of pollen grains collected by each bee species, indicates food amount harvested from plant taxa identified by pollen morphology, but nectar use is ignored. Combination of flower visitation and pollen diet provides proper estimation of floral resource use, but there has been no such study in the tropics. This study is the first case that investigate both in the same rainforest.

To find resource partitioning in feeding guild structure, cluster analyses were performed for stingless bees and plants based on overlap of pollen source taxa and flower-visiting stingless bee species, respectively. From floral features of the partitioned plants, I deduced interspecific variations of foraging traits related to the floral resource partitioning.

3.2 Materials and methods

Pollen diet

Pollen loads carried by returning foragers of 16 of the 26 colonies including seven

CBPS described four floral features of the plants from which flower visitors were collected (Momose et al. 1997). Floral location was categorized into three classes: 1) understory (<12.5 m high in the closed forest), 2) canopy (≥12.5 m high above the understory), and 3) gap (outside of the closed forest). Floral color was categorized into 1) white or green, 2) yellow, and 3) reddish (including orange, brown, red, pink and purple). Floral shape was divided into 1) cup or rotate, 2) brush, and 3) deep (including papilionaceous, Caesalpinia-like, campanulate, bilabiate, urceolate, tubular and chamber). Pollinators were classified into 1) eusocial bees (honey bees and stingless bees), 2) solitary bees (halictid, megachilid and anthophorid bees), and 3) others (beetles, butterflies, moths, cockroaches, diverse insects, birds and wind).

Data analysis

I determined Pianka's overlap indices for pollen diet and flower visitation (Pianka 1973). I calculated pollen diet overlap among bee species from assemblages of bee individuals with pollen types, and flower visitor overlap among plant species from assemblages of bee individuals collected at flowers. Cluster analyses based on these overlap indices for bees and plants were performed by UPGMA method. To determine plant families whose pollen was used by particular bees, I compared % foragers with pollen types of each plant family among stingless bee species by Kruskal-Wallis test. To determine stingless bee species which visited flowers of particular plants, I compared % visitors of stingless bee species among plant clusters by Kruskal-Wallis test. To characterize floral features of plant clusters, I compared distribution of plant species in the classes of the each floral feature between a plant cluster and all the other clusters by Fisher's exact probability test. For dichotomy comparison, I combined any two of the three classes.

3.3 Results

Pollen diet

Table 2. Percentages of returning foragers of seven stingless bee species, which carried pollen loads containing 107 pollen types of 21 plant families and unknown taxa.

Plant family	No. of pollen types	Stingless bee species[a]							P[b]
		fus	*lae*	*col*	*fim*	*ruf*	*mla*	*mli*	
Anacardiaceae	1	0	0	0	0	0	0	0	-
Annonaceae	10	0	0	0	0	4	34	7	**
Araceae	6	0	0	0	0	0	2	38	**
Aristolochiaceae	1	0	0	0	0	0	13	1	-
Compositae	1	0	0	0	0	1	0	0	-
Cucurbitaceae	3	0	0	4	0	21	0	0	-
Cyperaceae	2	0	0	6	0	4	3	0	-
Elaeocarpaceae	1	0	0	0	0	3	0	0	-
Ericaceae	1	0	0	0	0	0	1	0	-
Euphorbiaceae	5	63	55	16	38	27	8	17	-
Graminae	4	1	0	2	0	1	1	0	-
Leguminosae	2	0	2	16	38	1	1	0	-
Loranthaceae	1	0	0	0	0	0	1	1	-
Malvaceae	1	0	0	0	0	4	0	0	-
Melastomataceae	3	0	17	9	0	1	1	2	-
Onagraceae	1	0	0	0	0	0	1	1	-
Palmae	9	0	0	0	0	0	10	13	**
Passifloraceae	1	0	0	10	0	13	0	0	-
Plumbaginaceae	1	0	0	7	0	5	0	0	-
Rubiaceae	1	0	0	0	0	0	5	2	-
Urticaceae	4	21	2	5	0	0	2	5	-
Unknown	48	12	24	23	23	14	18	13	-
No. of foragers		209	42	239	26	77	119	128	

a: Species names are shown in Table 1.

b: Significance of difference in % foragers with pollen types of each plant family among stingless bee species. Kruskal-Wallis test; **: $P \leq 0.01$, -: $P > 0.05$.

Cluster analysis showed that *T. melina* and *T. melanocephala* had small (<0.26) overlap with other species (Fig. 7). Percentages of pollen foragers, which carried pollen of Araceae, Annonaceae and Palmae, were significantly different among stingless bee species (Kruskal-Wallis test: $P \leq 0.01$; Table 2). Pollen of these plant families was

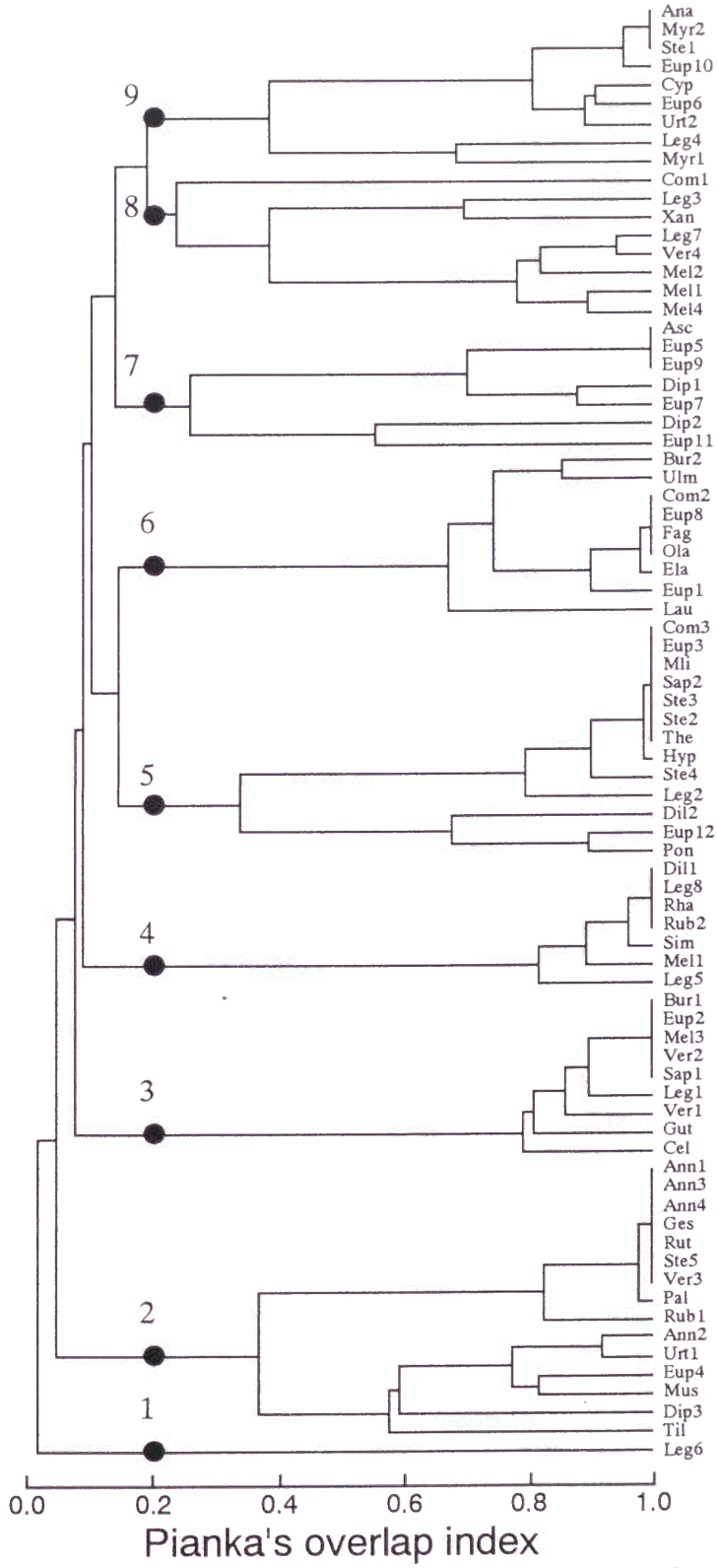

Fig. 8: A dendrogram showing Pianka's overlaps of flower-visiting stingless bee species among 78 plant species. Nine clusters are distinguished at 0.2 overlap index.

canifrons dominated Cluster 4 including leguminosae plants. *T. itama* were abundant in Cluster 5 including sterculiaceous species. *T. ventralis* and *T. moorei* mainly visited flowers of Cluster 6. *T. fimbriata* and *T. haematoptera* mainly visited flowers of Cluster 7 dominated by plants of Euphorbiaceae and Dipterocarpaceae. *T. erythrogastra* was major visitors of Cluster 8 dominated by plants of Melastomataceae and Leguminosae. Plants of Cluster 9 were mainly visited by *T. fuscobalteata*.

Floral features

Floral location of plant species of Cluster 2 significantly differed from species of all the other clusters (Fisher's exact probability test: $P \leq 0.01$; Table 4). Twelve of 15 plant species of Cluster 2 had understory flowers. Floral color of plant species of the any clusters did not significantly differed from the other clusters ($P > 0.05$; Table 5). Floral shape of plant species of two clusters significantly differed from the other clusters ($0.01 < P \leq 0.05$; Table 6). Plants of Cluster 3 had cup, rotate or brush flowers. On the other hand, plants of Cluster 8 had deep flowers. Pollinators of plant species of three clusters significantly differed from the other clusters ($P \leq 0.05$; Table 7). Plants of Clusters 2, 3 and 8 were pollinated by non-bee vectors, eusocial bees and solitary bees, respectively.

Table 6. Number of plant species of nine plant clusters with three floral shapes.

Plant cluster	Floral shape			Comparison[a]	P[b]
	Cup or rotate	Brush	Deep		
1	0	0	1	Cup+Brush/Deep	-
2	7	1	7	Brush/Cup+Deep	-
3	5	4	0	Cup+Brush/Deep	*
4	3	1	3	Brush/Cup+Deep	-
5	7	2	4	Brush/Cup+Deep	-
6	5	3	1	Cup+Brush/Deep	-
7	3	3	1	Cup+Brush/Deep	-
8	1	1	6	Cup+Brush/Deep	*
9	1	5	3	Brush/Cup+Deep	-
	32	20	26		

a: Combination of floral shapes used for comparison of plant species distribution.

b: Distribution was compared between a plant cluster and the rest all. Fisher's exact probability test; *: $0.01 < P \leq 0.05$, -: $P > 0.05$.

Table 7. Number of plant species of nine plant clusters with three pollinators.

Plant cluster	Pollinator			Comparison[a]	P[b]
	Social bees	Solitary bees	Others		
1	1	0	0	Social bees/Solitary bees+Others	-
2	3	2	10	Social bees+Solitary bees/Others	**
3	8	0	1	Social bees/Solitary bees+Others	*
4	4	1	2	Social bees/Solitary bees+Others	-
5	7	5	1	Social bees+Solitary bees/Others	-
6	6	1	2	Social bees/Solitary bees+Others	-
7	5	0	2	Social bees/Solitary bees+Others	-
8	1	6	1	Solitary bees/Social bees+Others	**
9	2	2	5	Social bees+Solitary bees/Others	-
Total	37	17	24		

a: Combination of floral shapes used for comparison of plant species distribution.

b: Distribution was compared between a plant cluster and the all rest. Fisher's exact probability test; **: $P \leq 0.01$, *: $0.01 < P \leq 0.05$, -: $P > 0.05$.

3.4 Discussion

The results showed three distinctive types of floral resource use in a stingless bee guild

also had plant clusters whose flowers mainly visited by each of them. Foragers of these species exclude other foragers from their feeding patches, and exclusively foraged the occupied patches. In the consequence, flowers mostly visited by one of the aggressive species were often observed. Species with different aggressiveness partition flower patches of conspecific plants based on local flower density (Johnson and Hubbell 1975; Johnson 1981). However, partitioning of plant species by difference in aggressiveness has not been clearly demonstrated. This study also showed that pollen diet of aggressive *T. fimbriata* was similar to non-aggressive species.

The third type was foraging by *T. erythrogastra* for deep flowers with morphologically protected nectaries. These flowers belong to Melastomataceae and Leguminosae, which were legitimately pollinated by solitary bees (Appanah 1990; Momose et al. 1997). Hence, *T. erythrogastra* may be nectar thief from flowers pollinated by long-tongued solitary bees, such as leaf-cutting bees and carpenter bees.

Stingless bees have been regarded as generalists with high interspecific overlap in floral resource use, but the results suggest floral partitioning of plant taxa among stingless bee species. Flowers of the partitioned plants had different features. These unique floral features suggest that foraging traits of stingless bees also differ among species. In following chapters, I examined variations in foraging traits of stingless bees expected from floral features of partitioned plants.

rewards, being produced slowly over a long period (Kato 1996). Consequently, we expect that aggressively-defending species forage in upper strata, and that unaggressive species forage in lower strata.

Aggressive behavior of palaeotropical social bees has been poorly investigated in forests. Visitation of eusocial bees to artificial feeders were observed in Sri Lanka (Koeniger and Vorwohl 1979) and Peninsular Malaysia (Khoo 1992). They showed that aggression of stingless bees compensated the disadvantage due to smaller foraging area than that of honey bees, and that more aggressive stingless bees arriving later at feeders excluded unaggressive bees. These studies, however, were not designed to investigate how aggressive foraging affects floral resource partitioning among species of a local bee guild.

In this chapter, I show which kinds of the floral resource partitioning mentioned above are created by aggressive defense of flower patches. I have three aims: 1) to measure dominance hierarchy in aggressive foraging among social bee species, 2) to detect resource partitioning in time, height and quality of resources, and 3) to examine negative correlation between the aggressive dominance and superior position on the resource axes partitioned, which indicates trade-offs between foraging traits. Finally I discuss potential factors of trade-offs that bear the resource partitioning.

4.2 Materials and methods

Observation at flowers

Foraging of stingless bees was observed at flowers of a male tree of *Santiria laevigata* form. *glabrifolia* (Burseraceae; Fig. 10). The flowers bloomed at 35 m high above the ground in November 1994 in the canopy biology plot. I collected flower-visiting insects by a hand net for 10 min at seven times from 7:00 to 16:30 on 17 November 1994. Aggressive behavior of bees at the flowers was observed at each collection time. The

with diameter of 6 cm and height of 15 cm. I perforated six holes at the bottom edge of each bottle. I completely sealed the bottles except for the holes to prevent honey-water from flowing away, unless bees imbibed honey-water through the feeding holes. The total amount of honey-water in a feeder was enough so that potential reward remained constant during the experiments. Each feeder was set on a yellow pan located on the towers.

To examine possible temporal partitioning, I measured visitation rate (the number of bees visiting a feeder per min) of each species for 5-min observations at 1-4 hours intervals during daytime for up to 6 days after the presentation of feeders (Table 8). To examine possible partitioning in height and quality, the feeders with various sucrose concentration between 10 and 70%, and with two different diameters (0.2 and 0.7 mm) of feeding holes, were set at different heights (1-50 m above the ground) on the towers. Three experiments were conducted at the two towers between Feburary and October in 1994 (Table 8).

two consecutive observations. Decrease in the visitation rate was tested by two-tailed one-sample t-test.

I tested whether four measures: 1) time of the first arrival after feeder presentation except for night time, 2) height of the visited feeders above the ground, 3) sucrose concentration of honey-water of visited feeders, and 4) size of feeding holes of visited feeders, differed among species, using ANOVA with two factors, species and experiments (Statsoft 1992). Significant differences in the measures on feeder use between any species pairs were examined by Scheffe's multiple comparison test.

I ranked bee species in aggressive dominance, based on both the aggressive behavior and the asymmetric change in the visitation rates after encounters. To show positions of species on the four resource axes, I ranked species along the axes from superior to inferior position: 1) time of the first arrival: from earlier to later, 2) height of feeders: from higher to lower, 3) sucrose concentration: from higher to lower and 4) size of feeding holes: from larger to smaller. To detect negative correlation between aggressive dominance and superior position on each resource axis, I examined the associations between these ranks by Kendall rank correlation.

4.3 Results

Observation at flowers

Individual flowers of a male tree of *Santiria laevigata* opened before 7:00 and bloomed for 1-1.5 day. Flowers produced both nectar and pollen as rewards. Sucrose production rate reached a plateau (6.3 mg/h) at 9:00-12:00, and standing amount of sucrose increased until 9:00 and remained at 5.9-6.4 mg until 16:00 (Fig. 11a). Sucrose concentration increased from 10% to 60% at 9:00, and reached to 70% in the afternoon (Fig. 11b). The number of pollen grains in a flower was 6000-9000 at 7:00 before anther dehiscence, and constantly decreased to 2500 in the late afternoon (Fig. 11c).

I collected 444 insect visitors in five orders on *S. laevigata* flowers. Stingless bees (13 species) were the most abundant (71% in individuals) among the visitors. *T. canifrons* behaved aggressively on the flowers. Hovering above the flowers, *T. canifrons* turned to face newly arrived bees of other species and chased them. I did not observe *T. canifrons* attacking conspecific foragers, suggesting that they were nestmates. Other bee species did not show aggressive behavior during the observations.

Visitation of *T. canifrons* peaked from 9:00 to 12:00 when nectar production reached a plateau (Fig. 11d). In contrast, *T. itama*, *T. collina* and *T. apicalis* mostly visited the flowers before 9:00 (Fig. 11e). *T. itama* visited the flowers again after 15:00 when *T. canifrons* stopped foraging. Three species in subgenus *Lepidotrigona*, *T. ventralis*, *T. terminata* and *T. nitidiventris*, visited flowers throughout a day, not affected by the presence of *T. canifrons* (Fig. 11f).

Feeder experiments

At the feeders, I found 12 stingless bee species and one honey bee species (Table 9). Among the 13 species, the top seven species in abundance were analyzed in detail. Among them, *Trigona fimbriata*, *T. apicalis* and *T. melina* were aggressive to other bee species (Table 10). *Apis koschevnikovi* was aggressive only to conspecifics.

guard bees stayed at the feeders, and two or three guard bees faced toward a feeding hole from 5 mm. These guard bees stayed at the feeders for 5-15 min and infrequently imbibed honey-water, while other nestmates foraged, staying only for 1-2 min. When guard bees of *T. fimbriata* were on the feeders, other bees left without attempting to land.

T. apicalis displayed threat to unaggressive species in the same way as *T. fimbriata*. No encounter between *T. apicalis* and *T. melina* was observed.

T. melina threatened other bee species less frequently than *T. fimbriata* and *T. apicalis*. *T. melina* often bit rival bees on neck and legs, and brought up the body of the rivals, and then removed them from the feeders. In spite of the direct body contact, the removed bees were rarely injured. After *T. melina* monopolized the feeders, two or three guard bees defended a feeding hole and stayed for 3-10 min. However, they were unable to exclude completely invasion of larger bees.

A. koschevnikovi faced and rushed to others, when >5 honey bees rushed to the same feeding hole. Aggression of honey bees was exhibited when imbibing was interrupted by other conspecific foragers.

Aggressive species, *T. fimbriata*, *T. apicalis* and *T. melina*, did not significantly decrease their visitation rates after encounters with honey bees and unaggressive stingless bees (Table 11; $P > 0.05$; one-sample t-test). Visits of *A. koschevnikovi* became significantly fewer after encounters with *T. fimbriata* ($P < 0.01$), but were less affected by encounters with *T. melina* and unaggressive stingless bee species. Unaggressive species, *T. ventralis*, *T. laeviceps* and *T. melanocephala*, reduced their visitation rates after encounters with all the other bee species. Decreases in visitation rates of *T. laeviceps* and *T. melanocephala* were significant ($P < 0.05$) in eight of 11 cases, but those of *T. ventralis* were not significant ($P > 0.05$) in any of five cases.

feeders (<15 m). *T. apicalis* and *T. melina* showed intermediate foraging height. An interaction between species and experiments was also significant ($F = 5.09$, $df = 7$, $P < 0.0001$). *T. melanocephala* always visited the lowest feeders, and that *T. melina* visited lower feeders when aggressive bees visited higher feeders.

Table 13. Height above the ground of feeders visited by seven eusocial bee species. No significant ($P > 0.05$) difference between same letters

Species	No. of observations	Mean ± SD (h)	Scheffe comparison
kos	344	27.9 ± 15.6	ab d
fim	89	26.7 ± 7.27	abcd
lae	381	24.5 ± 17.6	abcd
mli	111	21.7 ± 19.5	bcde
api	15	18.9 ± 8.96	abcdef
ven	78	14.9 ± 13.6	cdef
mla	132	12.2 ± 16.5	def

Two measures of energetic quality of visited feeders: sucrose concentration of honey-water and size of feeding holes did not significantly differed among the species ($F = 0.37$, $df = 6$, $P = 0.898$; $F = 1.93$, $df = 4$, $P = 0.104$, respectively).

Based on the evidences shown above, I ranked the seven bee species in aggressive dominance and position on the two resource axes partitioned among the species: arrival time and foraging height (Table 14). The time of the first arrival at feeders had significant negative correlation with the aggressive dominance (Kandel rank correlation coefficient $\tau = -0.67$; $P = 0.035$), but the height of visited feeders did not ($\tau = 0.31$; $P = 0.33$).

by the attacked scouts may cause decrease in visitation to the feeding sites. Temporal displacement of bee visitors of *Santiria* flowers also suggests that interference competition occurs at forest canopy.

The subgenus *Lepidotrigona* was robust to interference of aggressive stingless bees, which may be insinuation described by Johnson (1982). Because different behavior of aggressive species to *Lepidotrigona* were not observed, *Lepidotrigona* seems to use resources unavailable for aggressive species to avoid interference competition. Our observations that *Lepidotrigona* can lick up viscous nectar due to their flatter labium support this hypothesis (Chapter 5).

Resource partitioning

I detected interspecific partitioning of the feeders in time and height but energetic quality. At canopy flowers, however, temporal replacement of bee species depended on nectar production rate per flower. These conflicting results may come from difference between the artificial feeders and the natural flowers, in particular, the smaller scale of our feeder presentation (<30 feeding holes on a 25 m^2 tower) than the observed flowers (>10000 flowers on 80 m^2 foliage; Roubik 1993).

Time of the first arrival at feeding site and energetic quality of foods have been regarded as main resource axes partitioned among eusocial bee species (Johnson and Hubbell 1975; Hubbell and Johnson 1978; Roubik 1980). In contrast, interspecific partitioning in foraging height in the forest profile may be unique to dipterocarp forests in Sarawak (Roubik 1993; Roubik et al. 1995). Experiments using standardized feeders suggests that *T. melanocephala* specialized not to specific flowers in the understory, but to lower foraging strata. Pollen diet and flower visitation showed that *T. melanocephala* and *T. melina* used understory flowers (Chapter 3). I regarded *T. melina* as facultative understory foragers because they foraged at upper strata when aggressive foragers were absent. Prediction that aggressive species forage upper strata than unaggressive species

There are four possible factors to cause later arrival of aggressive species at the feeders: 1) long foraging distance due to low density of colonies, 2) small population size of colonies, 3) small allocation of foragers for scouting, 4) low searching efficiency of individual scouts. Among these, 1) is supported but 2) is rejected by a survey of eusocial bee nests in Sumatra (Salmah et al. 1990). In the canopy biology plot, colonies of aggressive species, *T. fimbriata* and *T. melina*, found to be nearer to towers where feeder experiments were conducted than some colonies of unaggressive species (Fig. 10). Thus the factor 1) hardly caused the later arrival of the aggressive species in the study. The factor 3) seem to play more important role than the factor 4) if aggressive species have communication and recruitment systems which favor occupation of flower patches. Requirement of recruits and guards to the patches already discovered may make scouts searching newly available patches fewer. To examine the factors 3) and 4), comparative observations of both organization of foragers and behavior of individuals should be conducted (Inoue et al. 1985).

melina and *T. melanocephala* used understory flowers pollinated by non-bee vectors. *T. erythrogastra* are expected to have longer tongues and slender heads. Among shallow-flower users, canopy-foragers may encounter more viscous nectar, because sunlight evaporates water in nectar of shallow flowers. Thus canopy-foraging species may collect nectar in higher sugar concentration, and have hairier and flatter glossae suitable to pick up viscous nectar compared to understory-foraging species, *T. melina* and *T. melanocephala*.

To test the predictions mentioned above, I analyzed interspecific morphological variation in 17 stingless bee species and sugar concentration of nectar loads of six species, whose floral resource use had been investigated. Based on this analysis, relationships between morphological variation and resource partitioning are explained.

5.2 Materials and methods

Morphological analysis

To summarize interspecific morphological variation in 17 stingless bee species (Table 1), seven characters of five individuals of each species were measured by a micrometer of a light microscope (Fig. 12). All measured bees were collected from the plot. The length of prementum (PL) and glossa (GL) may be related with accessibility to deep flowers. Mouthpart width (the distance between the bases of the mandibles: MW), head length (HL), and head width (HW) may also affect accessibility to flowers. Wing length (WL) as the distance between the apical tip and the base of the forewing seems related with flight ability. Corbicular length (CL) was measured to access the capacity of pollen loads. Using canonical discriminant analysis, stingless bee species were discriminated by the seven characters (Statsoft 1992). Coefficients of the characters of linear functions for the first and second canonical variables which maximize interspecific variation were calculated.

5.3 Results

Morphological analysis

Morphological variation among the 17 species was shown on coordinates of the first two canonical variables, C_1 and C_2, that represented 73% and 22% of the total variation, respectively (Fig. 13). Most species had small intraspecific morphological variation, and were clearly discriminated by the seven morphological characters (Table 15). Among the characters, PL, WL, CL, and GL had larger standardized coefficients C_1 and C_2 of the first two canonical variables. The coefficients of each characters were shown as vectors (C_1, C_2) on Fig. 13. Vectors of PL and GL, that had similar directions, indicated that longer-tongued four species, *T. thoracica*, *T. erythrogastra*, *T. itama*, and *T. nitidiventris*, were in a quadrant with (-, +) coordinates, and shorter-tongued species were in other quadrants. Among the shorter-tongued species, seven smaller and six larger species were over and under $C_1 = -C_2$, respectively, because vectors of WL and CL, that indicated body size, had (-, -) directions. Vectors of head parts, HL and MW, were small in opposite directions to body size, WL and CL. This indicated that larger species had heads relatively smaller than wings and legs.

tongued four species, particularly *T. thoracica* and *T. erythrogastra*, had less hairy and/or tubular glossae. Most shorter-tongued species had hairy glossae, except for *T. terminata* and *T. moorei*, which had slightly longer tongues among smaller species (Fig. 13). Among the 11 species with short and hairy tongues, the larger six species, *T. fimbriata*, *T. canifrons*, *T. apicalis*, *T. melanoleuca*, *T. collina*, and *T. rufibasalis*, had flat glossae. The smaller four species, *T. fuscobalteata*, *T. melina*, *T. melanocephala*, and *T. laeviceps*, had tubular glossae, except for *T. ventralis* with a flat glossa, which mainly visited brush flowers.

foraging species, *T. fuscobalteata*, (45 ± 13%; Scheffe test, P = 0.032). Large species, *T. fimbriata*, also used nectar in lower sugar concentration (26 ± 10%) than *T. fuscobalteata* (P < 0.001) and *T. collina* (40 ± 15%; P = 0.012). Insignificant interaction between species and time indicated that patterns of temporal changes in nectar sugar concentration were not different for the stingless bee species (Table 16). The nectar sugar concentration significantly increased from the morning to the afternoon (Table 16, Fig. 15).

Table 16. Analysis of variance for sugar concentration of nectar loads brought to colonies of six stingless bee species.

Source	df	MS	F	P
stingless bee species	5	825.9	5.63	<0.001
time of day	2	1336.2	9.12	<0.001
species x time	10	165.2	1.13	0.346
Error	155	146.6		

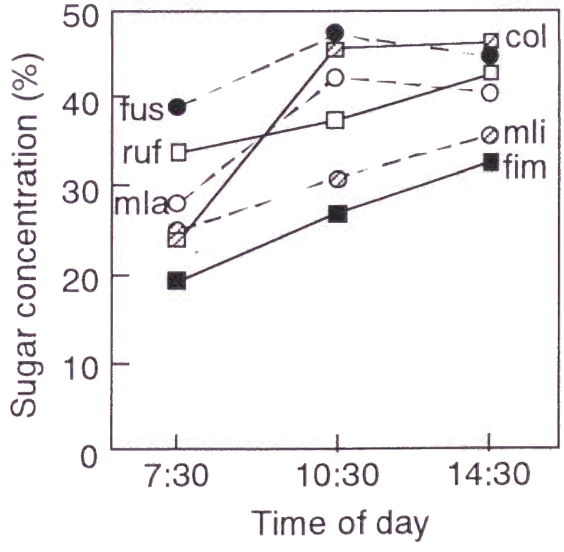

Fig. 15: Temporal changes in sugar concentration of nectar loads of six stingless bee species. Species codes are shown in Table 1.

5.4 Discussion

Floral shape and tongue length

I found that a stingless bee species, *T. erythrogastra* which visited deep flowers with

lower sugar concentration than a canopy-foraging species, but sugar concentration of nectar loads of *T. melanocephala* did not differ from those of other species. This unclear result suggests that sugar concentration of floral nectar available to stingless bees did not differ between sunny and shaded places, and/or that the understory-foraging species also collected nectar from sunny places. The result that increase in nectar sugar concentration from the morning to the afternoon probably due to evaporation were found in understory-foragers supports the latter possibility (Inoue et al. 1985).

Nectar sugar concentration may be related not with foraging stratum, but with aggressive behavior to defend foraging sites (Johnson and Hubbell 1974). *T. fimbriata* and *T. melina*, which used the most dilute nectar, were aggressively-foraging species, and other four species were not aggressive (Chapter 4). A neotropical aggressive stingless bee species, *T. corvina*, did not discriminate sugar concentration of artificial feeders in small patches, because they were group-foragers and occupied all feeders (Roubik et al. 1995). Thus local distribution of nectar sources may be more important than energetic quality of the each nectar source as a determinant of profitability of aggressive foragers.

The flatter glossae of short-tongued species foraging at canopy and gaps support the prediction that a flat glossa may suit to pick up more viscous nectar. On honey-sprayed leaves, *T. ventralis* was often observed to remain foraging until honey became dry (Chapter 4). However, the analysis of nectar loads did not show that species with flatter glossae used nectar in higher sugar concentration. *T. fimbriata* with a flat glossa used dilute nectar, while *T. fuscobalteata* with a tubular glossa used concentrated nectar. These results suggest that flatness of the glossa does not affect efficiency to imbibe nectar in higher sugar concentration, and that the shape of the glossa has other functions.

Table 17. Pollen diet similarity (Jaccard's index) among stingless bee species in four sites: Lambir in Malaysia (Present study), Anuradhapra in Sri Lanka (Koeniger and Vorwohl 1979), Chiapas in Mexico (Martinez-Hernandez et. al. 1994) and Gamboa in Panama (Roubik 1986). Vegetation types of these sites are shown.

	Sites			
	Lambir	Anuradhapra	Chiapas	Gamboa
Vegetation				
pastures			+	
farms		+		
orchards			+	
secondary forests	+	+	+	+
primary forests	+			+
No. of plants species	104	46	71	48
No. of stingless bee species	7	4	4	10
Mean similarity	0.10a	0.34b	0.25b	0.31b

a, b: Same letters mean insignificant differences

6.2 Variations in foraging traits and heterogenieties of floral resources

Spatial, temporal and morphological partitioning of floral resources were found in LHNP. These types of resource partitioning correspond with common resource axes, habitat, time and food type, recognized in the past (Schoener 1974). The partitioning comes from interspecific variation in behavioral and morphological foraging traits. Interspecific variations of these traits were related to spatial and morphological heterogeneities and temporal fluctuation of floral resources.

Spatial partitioning

Partitioning of feeding location has been frequenly reported from nectarivores. Two types of spatial partitioning: teritoriality and feeding habitat selection, are prevalent (Pyke 1979; Willmer and Corbet 1981).

Feeding territories are observed in hummingbirds and honeycreepers (Carpenter and MacMillen 1976; Kodric-Brown and Brown 1978; Pyke 1979). Defence of territory spend enegry of aggressive behavior. Thus energetic balance of benefit and cost determined size of territories. For central place foragers such as eusocial bees, feeding territories around nests result in nest spacing, which was observed in the neotropics

observed in seed-feeding desert rodents (Ziv et al. 1993). In a case of non-aggressive bee species, foraging overlaps were observed in nectar-rich periods, and then species with higher foraging cost ceased foraging as nectar was consumed (Schaffer et al. 1979). In aggressive stingless bees, spatial partitioning between dense and sparse flower patches was thought to come from the same mechanisms (Johnson and Hubbell 1975). In this study, aggressive *T. canifrons* visited *Santiria laevigata* flowers when nectar production peaked, and excluded parts of other foragers from the flowers (Chapter 4). To confirm daily fluctuation of nectar production caused the temporal partitioning, I have to show *T. canifrons* had higher energetic cost than other foragers.

Similar temporal partitioning occurred at the standardized feedrs which alway suppy at the same rate of sucrose (Chapter 4). Thus resource fluctuation related to foraging efficiency did not cause temporal partitioning in this case. Previous observations of foraging behavior at feeders show both aggression which causes forager replacement and later arrival of aggressive foragers (Hubbell and Johnson 1978; Khoo 1992). Present study reveals a trade-off between aggressive dominance and searching ability in an eusocial bee guild (Chapter 4). This type of temporal partitioning requires both ephemeral floral patches which bees have to discover at each flowering duration and resource storage over flowering durations. These situations may agree with eusocial bees in tropical rainforests.

Morphological partitioning

Morphological partitioning based on matching between mouthparts and flowers is common in nectarivores (Heinrich 1976; Brown and Bowers 1985). However, morphological partitioning by stingless bees has not been reported before present study.

To date, morphological partitioning in eusocial bees was mainly studied in bumble bees (Heinrich 1979). Temperate bumble bee guild with 4-6 species in North America showed clear patterns that mean tongue length regularly differed among species, which

than stingless bees. Such commensalism, floral resource use from non-pollinated plants, has been often observed in neotropical eusocial bees (Roubik 1982).

In contrast to the commensalism, temporal partitioning of flowers by eusocial bees may facilitate pollination. Bees which were excluded by aggression from a flower patch have to search newly available flower patches. They tend to foraged another flower patch of conspecific plants because of floral constancy (Waser 1986). In this process, pollen transfer between plant individuals of the same species may be promoted. Another mechanism to facilitate pollen transfer by switching of foraging patches was caused by temporal changes in floral reward production. Several species of small stingless bees, numerically the major visitors of *Xerospermum intermedia* (Sapindaceae), foraged first for male trees, and then for trees with pistllate flowers, based on daily change in nectar quality (Appanah 1982).

6.4 Competition behind floral resource partitioning

Resource partitioning do not always come from competition (Schoener 1986). Random association of species from a species pool can produce pattern of resource partitioning and niche separation (Connor and Simberloff 1979; Lawlor 1980; Conner and Simberloff 1983). To reject the random precess, diet overlap or trait variation among species in local sites must be significantly larger than those among species randomly selected from a species pool. However, definition of species pools and neutral sampling from the species pool are difficult. In this study, I was not able to test the observed pattern of resource partitioning by neutral models. However, the study site had the highest species diversity in eusocial bee fauna in Southeast Asia (Chapter 2). Thus the observed resource partitioning may reflect patterns of a species pool in Asian eusocial bees. Below, I discussed interference and exploitative competition which may affect foraging success, population growth and evolution of foraging traits.

Interference competition by aggressive behavior reduced frequency of visits to

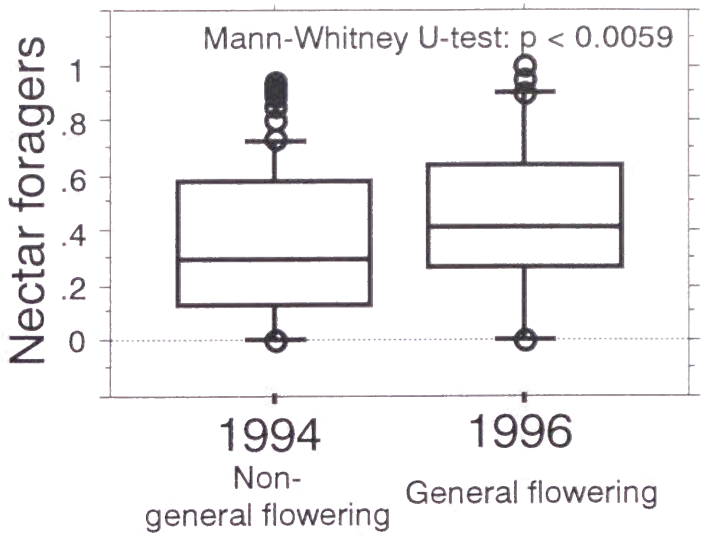

Fig. 17: Comparison of rate of foragers with nectar loads of six stingless bee species between in 1994 and 1996. 1994 was in an interval of general flowering occurred in 1992 and 1996. The rates in 1994 and 1996 are significantly differenct (Wilcoxon's test: P = 0.0059).

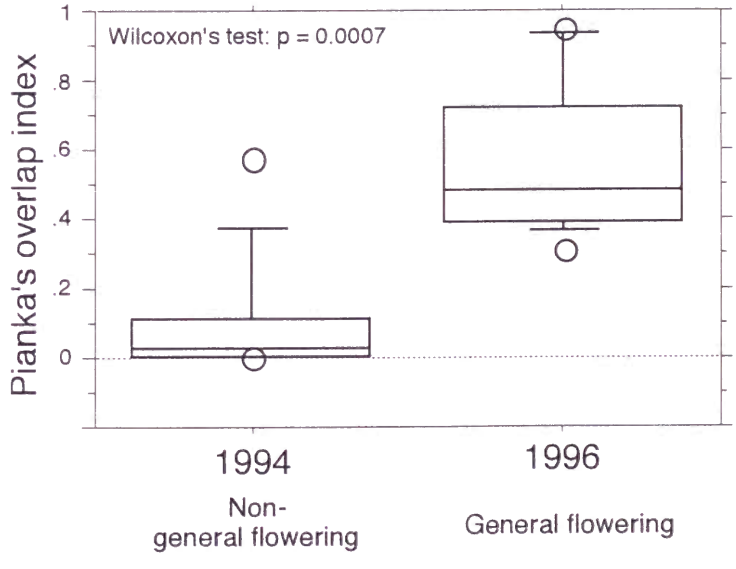

Fig. 18: Comparison of pollen diet overlap of six stingless bee species between in 1994 and 1996. 1994 was in an interval of general flowering occurred in 1992 and 1996. The overlaps in 1994 and 1996 are significantly differenct (Wilcoxon's test: P = 0.0007).

Colony dynamics during a general flowering cycle suggests that competition for floral resources may reduced suvival and reproduction of colonies (Chapter 2). Honey bees were disappearred during an interval between general flowering in 1992 and 1996, though their nest sites, branches of emergent *Koompasia* trees, tree holes and wooden

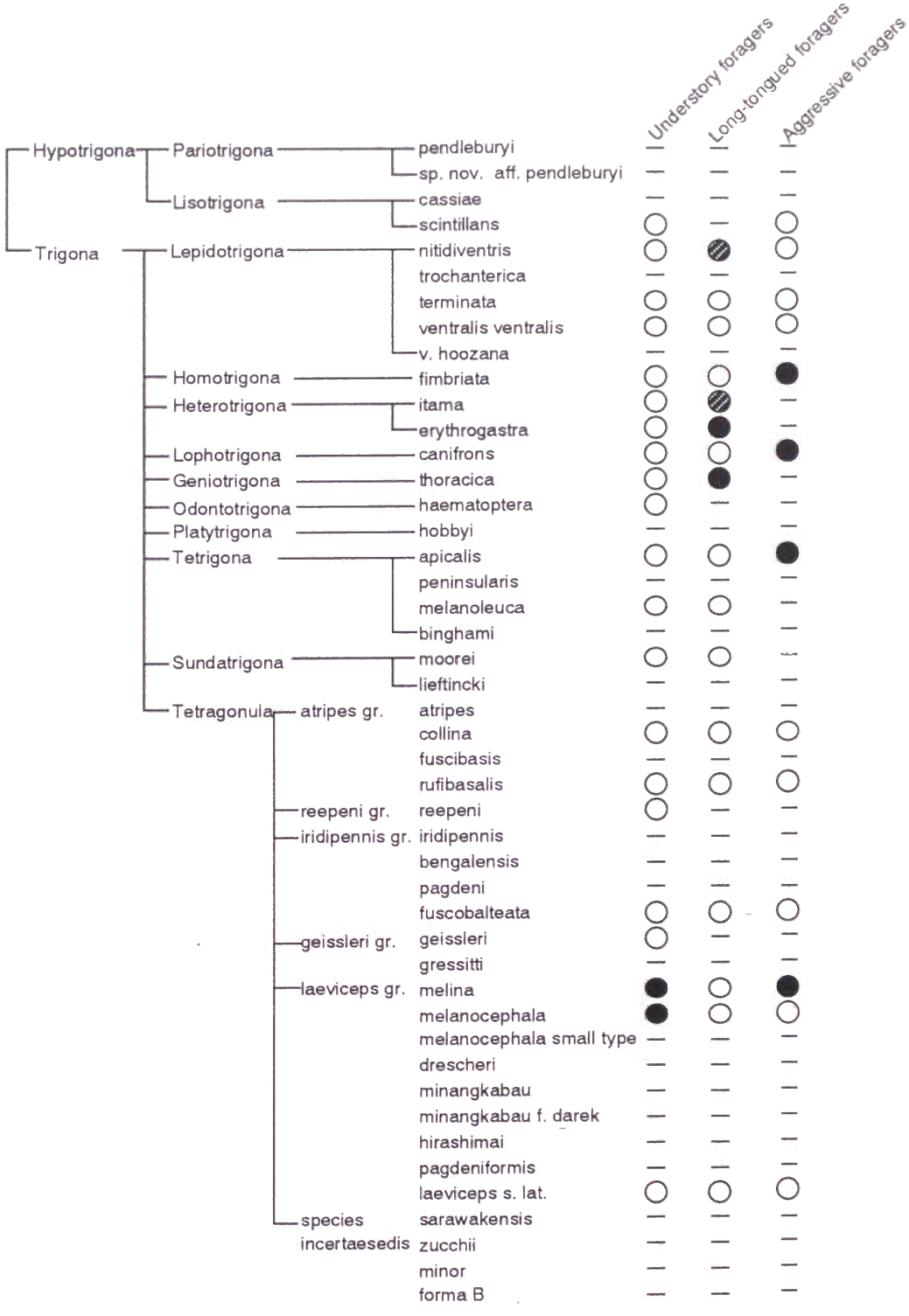

Fig. 19: Variation in foraging traits on taxonamic systematics of Southeast Asian stingless bee species. Solid and open circles mean presence and absence of the states of foraging traits shown in the top. Shaded circles means intermediate states between them. Hyphun means no infomation on the traits.

Abstract in Japanese （要約）

アジアの熱帯雨林における真社会性ハナバチによる花資源分割の群集生態学的研究

永光輝義（京都大学生態学研究センター）

熱帯の重要な送粉昆虫である真社会性ハナバチ、ハリナシバチとミツバチは利用する花資源が種間で重複するジェネラリストだとかんがえられてきた。本研究は、花資源の多様度がきわめてたかいマレーシア、サラワクの熱帯雨林において、真社会性ハナバチの種間に花資源の分割があることをしめし、その分割をもたらす採餌形質の種間変異と花資源の異質性をあきらかにした。

調査地では1992年と1996年に一斉開花がみられ、真社会性ハナバチの個体群は開花率の変化にともない変動した。ミツバチは一斉開花がおわると調査地から移出した。ハリナシバチの個体群は安定していたが、分封は一斉開花期におこった。

林冠観測システムをもちいた訪花昆虫の採集と巣にもちかえった花粉の同定によってハリナシバチが利用していた植物をあきらかにした。その結果、ことなる特徴の花を利用するハリナシバチの種(*Trigona* spp.)がみとめられた。*Trigona melina*と*T. melanocephala*は、ハナバチ以外に送粉される林床の花を利用した。 *T. erythrogastra*は、単独性ハナバチに送粉されるふかい花弁をもつ花を訪問した。花になわばりをはり他の採餌個体を排除する攻撃的種*T. apicalis*は、社会性ハナバチに送粉され皿状またはブラシ状の花をもつ植物の訪花を独占した。

人工の給蜜器をさまざまなたかさに設置した実験から、林床の花を利用した種は低高度の給蜜器をおもに利用することと、より攻撃的な種ほど給蜜器の発見がおくれることがわかった。後者は、真社会性ハナバチの間に餌場の防衛と発見とのトレードオフがあることを示唆した。そして、餌場におくれてやってきた種がさきに餌場を発見した種を排除するという餌場の時間的分割が林冠の花と人工蜜源でみられた。

ハリナシバチの口器の形態を分析した結果、ふかい花弁をもつ花を利用した種は体サイズにくらべて舌がながかった。しかし、利用した花蜜の糖度と下舌の形態との間には一貫した関係がみられなかった。

以上から、真社会性ハナバチの種が空間的、時間的、形態的に花資源を分割する機構は、採餌形質の種間変異とトレードオフおよびそれらに対応する花資源の異質性によって説明できた。さらに、これらの資源分割をもたらす干渉型の競争が給蜜器実験から示唆された。また、消費型競争の前提となる花資源の制限が、一斉開花時の採餌行動の変化と個体群動態から示唆された。

evidence for intraspecific competition. Oecologia 77: 522-525.

Endler, J. A. (1993) The color of light in forests and its implications. Ecological Monographs 63: 1-27.

Erdtman, G. (1960) The acetolysis method - a revised description. Sven. Bot. Tidskr. 54: 561-564.

Feinsinger, P., R. K. Colwell, J. Terborgh and S. B. Chaplin (1979) Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. American Naturalist 113: 481-497.

Fellers, J. H. (1987) Interference and exploitation in a guild of woodland ants. Ecology 68: 1466-1478.

Grant, P. R. (1986) Ecology and evolution of Darwin's finches. Princeton University Press, Princeton.

Harder, L. D. (1982) Measurement and estimation of functional proboscis length in bumblebees (Hymenoptera: Apidae). Canadian Journal of Zoology 60: 1073-1079.

Harder, L. D. (1983) Flower handling efficiency of bumble bees: morphological aspects of probing time. Oecologia 57: 274-280.

Harder, L. D. (1985) Morphology as a predictor of flower choice by bumble bees. Ecology 66: 198-210.

Harder, L. D. (1986) Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. Oecologia 69: 309-315.

Harvey, P. H. and M. D. Pagel (1991) The comparative method in evolutionary biology. Oxford University Press, .

Heinrich, B. (1976) Resource partitioning among eusocial insects: bumblebees. Ecology 57: 874-889.

Heinrich, B. (1979) Bumblebee Economics. Harvard University Press, Cambridge.

Heinrich, B. and S. L. Buchmann (1986) Thermoregulatory physiology of the carpenter bee, Xylocopa varipuncta. Journal of Comparative Physiology B 156: 557-562.

Heithaus, E. R. (1979) Communty structure of neotropical flower visiting bees and wasps: diversity and phenology. Ecology 60: 190-202.

Herrera, C. M. (1997) Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. Oikos 78: 601-611.

Hertel, H. and D. F. Ventura (1985) Spectral sensitivity of photoreceptors in the compound eye of stingless tropical bees. Journal of Insect Physiology 31: 931-935.

Huang, T. C. (1972) Pollen flora of Taiwan. National Taiwan University, Botany Department Press, Taipei.

Hubbell, S. P. and L. K. Johnson (1977) Competition and nest spacing in a tropical stingless bee community. Ecology 58: 949-963.

Hubbell, S. P. and L. K. Johnson (1978) Comparative foraging behavior of six stingless bee species exploiting a standardized resource. Ecology 59: 1123-1136.

Hutchinson, G. E. (1959) Momage to Santa Rosalia or why are there so many kinds of animals. American Naturalist 93: 145-159.

Inoue, T. and A. A. Hamid, Eds. (1994). Plant reproductive systems and animal seasonal dynamics of dipterocarp forests in Sarawak, the report of Monbusho international scientific research. Otsu, Center for Ecological Research, Kyoto University.

Inoue, T. and A. A. Hamid, Eds. (1997). General flowering of tropical rainforests in Sarawak, the report of Monbusho international scientific research. Otsu, Center for Ecological Research, Kyoto University.

Inoue, T. and M. Kato (1992) Inter- and intraspecific morphological variation in bumblebee species, and competition in flower utilization. pp. 393-427. In M. D. Hunter, T. Ohgushi and P. W. Price (eds.) Effects of resource distribution on animal-plant interactions. Academic Press, Orlando.

Kotler, B. P. and J. S. Brown (1988) Environmental heterogeniety and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19: 281-307.

Kotler, B. P., J. S. Brown and O. Hasson (1991) Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72: 2249-2260.

Kotler, B. P., J. S. Brown and A. Subach (1993) Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67: 548-556.

Kress, W. J. and J. H. Beach (1993) Flowering plant reproductive systems. pp. 161-182. In L. McDade, K. S. Bawa, G. Hartshorn and H. A. Hespenheide (eds.) La Selva: ecology and natural history of a neotropical rain forest. Chicago University Press, Chicago.

LaFrankie, J. V., T. Sylvester and P. S. Ashton (1995) Species list for the 52-ha forest dynamics research plot Lambir Hills National Park, Sarawak, Malaysia. Center for Tropical Forest Science Miscellaneous Internal Report 2.9.95.

Lawlor, L. R. (1980) Structure and stability in natural and randomly constructed competitive communities. American Naturalist 116: 394-408.

Losos, J. B. (1996) Phylogenetic perspectives on community ecology. Ecology 77: 1344-1354.

Martinez-Hernandes, E., J. I. Cuadriello-Aguilar, E. Ramirez-Arrga, M. Medina-Camacho, M. S. Sosa-Najera and J. E. Melchor-Sanchez (1994) Foraging of Nannotrigona testaceicornis, Trigona (Tetragonisca) angustula, Scaptotrigona mexicana and Plebeia sp. in the Tacaná region, Chapas, Mexico. Grana 33: 205-217.

McLellan, A. R. (1978) Growth anddecline of honeybee colonies and inter-relationships of adult bees, brood, honey and pollen. Journal of Applied Ecology 15: 155-161.

Michener, C. D. and D. W. Roubik (1993) Observations on the labium of meliponine bees (Hymenoptera: Apidae). pp. 251-266. In T. Inoue and S. Yamane (eds.) Evolution of insect societies: comparative sociology of bees, wasps and ants. Hakushin-sha Publishing Co., Tokyo, Japan.

Momose, K., T. Yumoto, T. Nagamitsu, M. Kato, H. Nagamasu, S. Sakai, R. D. Harrison, A. A. Hamid and T. Inoue (1997) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia I. Cahracteristics of the plant -pollinator community in a lowland dipterocarp forest. In T. Inoue and A. A. Hamid (eds.) General flowering of tropical rainforests in Sarawak, the report of Monbusho international scientific research. Center for Ecological Research, Kyoto University, Otsu.

Nieh, J. C. and D. W. Roubik (1995) A stingless bee (Melipona panamica) indicates food location without using a scent trail. Behavioral Ecology and Sociobiology 37: 63-70.

Pianka, E. R. (1973) The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

Pignata, M. I. B. and J. A. F. Diniz-Filho (1996) Phylogenetic autocorrelation and evolutionary constraints in worker body size of some neotropical stingless bees (Hymenoptera: Apidae). Heredity 76: 222-228.

Pimm, S. L. and J. W. Pimm (1982) Resource use, competition, and resource availability in Hawaiian honeycreepers. Ecology 63: 1468-1480.

Pyke, G. H. (1979) The economics of territory size and time budget in the golden-winged sunbird. American Naturalist 114: 131-145.

Pyke, G. H. (1982) Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. Ecology 63: 555-573.

Ranta, E. and H. Lundberg (1980) Resource partitioning in bumblebees: The significance of difference in

New York.

Sakagami, S. F., T. Inoue and S. Salmah (1990) Stingless bees of central Sumatra. pp. 201-218. In S. F. Sakagami, R. Ohgushi and D. W. Roubik (eds.) Natural history of social wasps and bees in equatorial Sumatra. Hokkaido University Press, Sapporo.

Sakai, S., K. Momose, T. Inoue and A. A. Hamid (1997) Climate data inLambir Hills National Park and Miri Airport, Sarawak. In T. Inoue and A. A. Hamid (eds.) General flowering of tropical rainforests in Sarawak, the report of Monbusho international scientific research. Center for Ecological Research, Kyoto University, Otsu.

Sakai, S., K. Momose, T. Nagamitsu, R. D. Harrison, T. Yumoto, T. Itino, M. Kato, H. Nagamasu, A. A. Hamid and T. Inoue (1997) An outline of plant reproductive phenology in one episode of general flowering cycle in 1992-1996 in Sarawak, Malaysia. pp. . In T. Inoue and A. A. Hamid (eds.) General flowering of tropical rainforests in Sarawak, the report of Monbusho international scientific research. Center for Ecological Research, Kyoto University, Otsu.

Salmah, S., T. Inoue and S. F. Sakagami (1990) An analysis of apid bee richness (Apidae) in central Sumatra. pp. 175-200. In S. F. Sakagami, R. Ohgushi and D. W. Roubik (eds.) Natural history of social wasps and bees in equatorial Sumatra. Hokkaido University Press, Sapporo.

Schaffer, W. M., D. B. Jensen, D. E. Hobbs, J. Gurevitch, J. R. Todd and M. V. Schaffer (1979) Competition, foraging energetics and the cost of sociality in three species of bees. Ecology 60: 976-987.

Schoener, T. W. (1974) Resource partitioning in ecological communities. Science 185: 27-39.

Schoener, T. W. (1986) Mechanistic approaches to community ecology: a new reductionism? American Zoologist 26: 81-106.

Schoener, T. W. (1986) Resource partitioning. pp. 91-126. In J. Kikkawa and D. J. Anderson (eds.) Community ecology: pettern and process. Blackwell, Melbourne.

Schwarz, H. F. (1939) The Indo-Malayan species of Trigona. Bulletin of American Museum of Natural History 90: 1-546.

Seely, T. D. (1985) Honeybee ecology. A study of adaptation in social life. Princeton University Press, Princeton, New Jersey.

Southwick, E. E. (1984) Photosynthate allocation to floral nectar: a neglected energy investment. Ecology 65: 1775-1779.

Statsoft (1992) STATISTICA User's guide 4.1J. Tulsa, Oklahoma.

Tissot, C., H. Chikhi and T. S. Nayar (1994) Pollen of wet evergreen forests of the western Ghats, India. Institute Francais de Pondichery, Pondichery (India).

Waser, N. M. (1986) Flower constancy: definition, cause, and measurement. American Naturalist 127: 593-603.

Willmer, P. G. and S. A. Corbet (1981) Temporal and microclimatic partitioning of the floral resources of Justicia aurea amongst a concourse of pollen vectors and nectar robbers. Oecologia 51: 67-78.

Wolda, H. and D. W. Roubik (1986) Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. Ecology 67: 426-433.

Ziv, Y., Z. Abramsky, B. P. Kotler and A. Subach (1993) Interspecific competition and temporal and habitat partitioning in two gerbil species. Oikos 66: 237-246.

Appendix 1. Number of returning foragers of seven stingless bee species carrying pollen loads of 107 distinguishable pollen types.

Pollen types	Plant family	Stingless bee species[a]							
		fim	col	ruf	fus	mli	mla	lae	Total
N1	Anacardiaceae				1				1
A21	Annonaceae					1			1
A30	Annonaceae					2			2
A36	Annonaceae					1	2		3
B3	Annonaceae						3		3
B9	Annonaceae					4	5		9
N2	Annonaceae						29		29
N3	Annonaceae			3					3
N30	Annonaceae						2		2
N31	Annonaceae		1						1
N4	Annonaceae					1			1
B18	Araceae					7			7
B2	Araceae					5	1		6
N5	Araceae					36			36
N6	Araceae				1				1
N7	Araceae						1		1
N8	Araceae					1			1
A3	Aristolochiaceae		1			1	15		17
N9	Compositae			1					1
B4	Cucurbitaceae		8						8
N10	Cucurbitaceae			15					15
N11	Cucurbitaceae		2	1					3
B15	Cyperaceae				1		2		3
N12	Cyperaceae		15	3			1		19
N13	Elaeocarpaceae			2					2
B10	Ericaceae						1		1
A13	Euphorbiaceae		6						6
B16	Euphorbiaceae	10	31	11	129	6	10	23	220
N14	Euphorbiaceae		2						2
N15	Euphorbiaceae					6			6
N16	Euphorbiaceae			10	3	10			23
B12	Graminae				3				3
C7	Graminae		1						1
N17	Graminae		4	1					5
N18	Graminae						1		1
N20	Leguminosae	10	37	1			1	1	50
N21	Leguminosae		1						1
N23	Loranthaceae					1	1		2
N24	Malvaceae			3					3
A10	Melastomataceae						1		1
C5	Melastomataceae		20	1		1		7	29
N25	Melastomataceae		1		1	1			3
N32	Onagraceae						2		2
A22	Palmae					2	1		3
A32	Palmae						2		2
B14	Palmae					1			1
B24	Palmae					6			6
N22	Palmae					3			3
N33	Palmae						1		1
N34	Palmae					3	2		5
N35	Palmae					1			1
N36	Palmae					1	6		7
N37	Passifloraceae		24	10					34
N38	Plumbaginaceae		16	4	1				21
N39	Rubiaceae					3	6		9
A17	Urticaceae				39	1		1	41
N27	Urticaceae		13		4		1		18
N28	Urticaceae					6			6
N29	Urticaceae						1		1
A1	Unkown						3		3
A11	Unkown		7				1		8
A14	Unkown		7						7
A15	Unkown		1	3					4
A16	Unkown			1					1
A18	Unkown				3				3
A19	Unkown				1				1
A2	Unkown						1		1
A20	Unkown							1	1
A23	Unkown	1							1
A23'	Unkown						1		1
A29	Unkown					1			1
A31	Unkown					1			1
A33	Unkown		4						4
A34	Unkown		1						1
A35	Unkown		1						1
A6	Unkown						1		1
A7	Unkown				1		1		2
A9	Unkown			2					2
B1	Unkown				3		2		5
B13	Unkown				2				2
B19	Unkown					7	2		9
B20	Unkown					1		1	2
B5	Unkown		2						2
B6	Unkown		1						1
B7	Unkown		14						14
C1	Unkown						1		1
C10	Unkown					2			2
C11	Unkown					2			2
C2	Unkown			1				8	9
C3	Unkown		2						2
C4	Unkown			1					1
C6	Unkown		4						4
C8	Unkown					1	2		3
C9	Unkown					1			1
N19	Unkown						1		1
N26	Unkown		1						1
N40	Unkown			2					2
N41	Unkown			1					1
N42	Unkown		1						1
N43	Unkown						2		2
N44	Unkown				1				1
N45	Unkown	1							1
N46	Unkown		9		14				23
N47	Unkown	4							4
N48	Unkown						3		3
N49	Unkown				1	1			2
N50	Unkown		1						1
Total		26	239	77	209	128	119	42	840

a: Species names of stingless bees are shown in Table 1.

Appendix 3. Number of flower-visiting stingless bees collected from 78 plant species.

Plants[a]	Stingless bee species[b]																				Total
	sci	nit	ter	ven	fim	ita	ery	can	tho	hae	api	mil	moo	col	ruf	ree	fus	gei	mli	mla	lae	
Ana																	4					4
Ann1																				1		1
Ann2																			3	2		5
Ann3																				1		1
Ann4																				8		8
Asc					1																	1
Bur1											2											2
Bur2	1	15	30	106		77	1	59			5			15			5	1	2		10	325
Cel		1									2						1					4
Com1							1							4			1					6
Com2			1	30									3									31
Com3						1																1
Cyp											1						4				4	9
Dil1		7			14			170						1		1	15		5		11	223
Dil2						1										1					1	2
Dip1		1			202	33	13	77			50			29	7	2	127				5	544
Dip2					27	7		1		31	23	20		6		4	3		1		2	121
Dip3																			1		1	2
Ela				12		2																14
Eup1				2							1											3
Eup2											7											7
Eup3						2																2
Eup4											2			1					2	3		8
Eup5					5																	5
Eup6																	9				4	13
Eup7		1	3	2	42	1				3				2			51		1		3	109
Eup8				5																		5
Eup9					6																	6
Eup10				2	2	2		3		8						1	30				1	48
Eup11				1			1			4												6
Eup12																					1	1
Fag				24																		24
Ges																				4		4
Gut		1				2	1		1		4											9
Hyp		17			2	422		58	3					43	9		34				4	592
Lau				1																	1	2
Leg1				1							2											3
Leg2		1	2		1	56	12		1					6	5		41	1	1	8	2	136
Leg3						1	1		22						3		7				2	36
Leg4	4					1											1					2
Leg5					1	1		6			1			1			4				1	15
Leg6								1				14										15
Leg7					1		37							1							1	40
Leg8								14														14
Leg9						1		2														3
Mel1						2	7										3					12
Mel2		1				17	20				4				3		3			1		49
Mel3											2											2
Mel4							1										1					2
Mli						3																3
Mus											1					2			3	3	1	8
Myr1	1			1													1					2
Myr2																	1					1
Ola				9							1						1					11
Pal											1									6	1	8
Pon						1															2	3
Rha								8														8
Rub1					4														1	6		11
Rub2								2														2
Rut																				1		1
Sap1											35									1		36
Sap2						1																1
Sim								3									1					4
Ste1																	1					1
Ste2				1		152											6				1	160
Ste3						1																1
Ste4					1	159	17	1						77	1							256
Ste5																				2		2
The						8	1										1					10
Til						2											1		3			6
Ulm			10	81		59							26		2		20			3	15	190
Urt1																			7	2	2	11
Urt2																	2			1	1	4
Ver1	2				1						4											5
Ver2											2											2
Ver3																				1		1
Ver4						1	4				1											6
Xan							1		1													2
Total	8	45	46	278	310	1016	118	405	28	46	151	34	29	186	30	11	379	2	30	54	77	3233

a: Species names of plants are shown in Appendix 2.
b: Species names of stingless bees are shown in Table 1.